

# HYBRIDIZATION BETWEEN NATIVE AND INVASIVE ALIEN PLANTS: AN OVERLOOKED THREAT TO THE BIODIVERSITY OF SRI LANKA

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## ABSTRACT

Conservation of native biological diversity is one of the major challenges of this century. Invasive alien species (IAS) are a part of this challenge because a small but a significant fraction of IAS contribute to the demise of native species. The present paper reviews current literature on the phenomenon of hybridization in plants supporting the evolution of invasiveness, which is identified as a major threat to the extinction of native species. Further, the phenomenon of hybridization is been reviewed on a Sri Lankan context by citing evidence from a preliminary study between the native *Nymphaea nouchali* and an introduced violet flowered water-lily that has got established in water-bodies of Sri Lanka. This violet flowered water-lily has been incorrectly identified as the native *Nymphaea nouchali*, the National flower of Sri Lanka ('Nil Manel'). Revealing the flawed identity of the violet flowered *Nymphaea*, its hybrid origin and the hybridization with the native *N. nouchali*, provides an excellent opportunity for initiating studies on a novel area in hybridization between natives and invasive alien species of plants in Sri Lanka.

**Key words:** biodiversity conservation, *Nymphaea*, evolution, 'Nil Manel', Invasive Alien Species (IAS)

Biological invasions are considered as serious threats to the biodiversity and presently ranked second only to habitat loss (Gurevitch and Padilla, 2004; Didham *et al.*, 2005; Tiebre *et al.*, 2007). However, according to Chapin *et al.* (2000), biological invasion may soon surpass habitat loss as the main cause of environmental degradation globally. This ranking has attracted greater attention towards Invasive Alien Species (IAS) in the last decade (Gurevitch and Padilla, 2004; Didham *et al.*, 2005; Tiebre *et al.*, 2007). Invasive Alien Species have the ability to compete with and replace native biota in natural habitats, thereby causing an immense threat to the native biological diversity. They possess special characteristics that enable them to spread fast and aggressively and compete with native flora and fauna, to form large populations that interfere with the ecological balance and the natural development of biotic communities. Generally IAS are identified under different terminologies such as 'exotics', 'aliens', 'non-natives', 'noxious', 'non-indigenous' or 'weedy' species, based on the approach and emphasis of the study (Colautti and MacIsaac, 2004).

## Biodiversity in Sri Lanka

Despite its relatively small land area of 65,610 km<sup>2</sup>, Sri Lanka harbours over 3,770 flowering plant species of which over a quarter are considered endemic to the island (IUCN Red Data List, 2007). Sri Lanka's varied climate and topography, has resulted in a rich biodiversity and the island is considered as one of the most biologically diverse areas in South Asia. The region including the Western Ghats of India and Sri Lanka together is considered as one of 34 biodiversity hotspots recognized in the world (Mittermeier *et al.*, 2005). These hotspots are areas that harbour an exceptionally high concentration of endemic species, but have already lost more than 75% of the primary vegetation (IUCN Red Data List, 2007). Of all the hotspots, the Western Ghats and Sri Lanka has the highest human population density (Cincotta *et al.*, 2000). The increase in human population on the island has resulted in the loss of biodiversity, due to anthropogenic factors such as habitat degradation and modification, over-exploitation of species, spread of invasive alien species and pollution (IUCN Red Data List, 2007).

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### **Invasive alien species and island flora**

According to Elton, (1958) and Donlan *et al.* (2003), islands have long been considered to be under intense ecological threat from the spread of invasive alien species. Sufficient evidence has emerged that IAS may now be the most significant drivers of population declines and species extinctions in island ecosystems globally (Veitch and Clout, 2002; Donlan *et al.*, 2003). Oceanic island floras are often disharmonic, with representation of families differing from that on the neighbouring mainland (Loope and Mueller-Dombois, 1989). In this context, introductions of IAS are of particular concern to Sri Lanka. In addition to being an island, several other factors such as smaller size, developing economic status, high levels of species endemism in the southwest of the country, highly threatened status of many endemic species and their habitats, and increased degradation and fragmentation of natural habitats due to development activities are few other factors that make IAS important (Clout, 1995; Marambe *et al.*, 2001).

### **Introduction of IAS to Sri Lanka**

The introduction of IAS into the country in the past, either by intentional or unintentional anthropogenic dispersal moves, has had a direct impact on the country's economy either as alien pests, or as weeds (Marambe *et al.*, 2001). Intentional introductions include deliberate introductions for use in agriculture, forestry, horticulture, fisheries, aquaculture, landscaping, zoological gardens, pet trade *etc.* and Sri Lanka has experienced several such incidents in the past. The Royal Botanic Gardens, Peradeniya has played a major role in many plant introductions where some plants, such as *Eichhornia crassipes* (E. Water Hyacinth, S. Japan-jabara), have become serious invaders (Wijesundara, 2001). *Salvinia molesta* is another plant introduced to the island in 1939 on scientific interest (Senaratna, 1943). Unintentional introductions include accidental introductions of species through transport, trade, travel, tourism, *etc.*, and the weed, *Parthenium hysterophorus* is one such alien species (Jayasuriya, 2001). The direct economic consequences of IAS are more prominent in the agricultural sector and irrigation systems, while the indirect impacts include a variety of human concerns relating to health, transportation, recreation and loss of biodiversity. However, in the recent years, more interest has been paid towards the introduction of IAS and their impacts on the local biodiversity.

### **Current research and future trends**

Many studies locally and globally, have been carried out covering different aspects of IAS, and also analysing and building up models for predicting future consequences.

Invasive alien species have attracted the attention of evolutionary biologists and ecologists because they represent historical examples of dramatic evolutionary and ecological changes. Many of the IAS species that become successful only do so either following an unusually long lag time after initial arrival, and/or after multiple introductions (Tiebre *et al.*, 2007; Ellstrand and Schierenbeck, 2006). Discussions on the population biology of invasives have focused largely on their ecology and the evolutionary consequences of the invasive process. Certain ecological explanations for invasiveness include encountering an unfilled niche (Williamson 1996), increased competitive ability relative to the native biota (Holway, 1999), unavailability of natural enemies (Callaway *et al.*, 2004) or ecological release (Ellstrand and Schierenbeck, 2006).

Perhaps the most frequently documented effects of IAS are their suppression of native populations through predation, competition, parasitism, or disease (Chornesky and Randall, 2003). However, the evolution of invasiveness as an adaptive trait has been less addressed (Ellstrand and Schierenbeck, 2006). Anderson and Stebbins (1954) and Abbott (1992) attribute invasiveness to the phenomenon of hybridization (Ellstrand and Schierenbeck, 2006 and reference there in). Few other evolutionary pathways to invasiveness have already received some attention. For example, weeds have evolved to mimic unrelated crops and have become successful invaders of agro-ecosystems (Barrett, 1983). Likewise, Jain and Martins (1979) witnessed a single gene mutation that is apparently answerable for the appearance of invasiveness in rose clover in California.

Ellstrand and Schierenbeck (2006), analysed the concept of hybridization to build up a possible model for the evolution of invasiveness. According to the model hybridization can, through one or more mechanisms catalyze the evolution of invasiveness. Human dispersal and disturbances together act to accelerate the process and increase the opportunities to take hold the hybrid lineages. However, it should be noted that only a fraction of hybridization events will lead to the evolution of invasiveness. In addition, they propose an evolutionary mechanism that may account for these observations. Hybridization between species or between disparate source populations may serve

as a stimulus for the evolution of invasiveness. Progeny with a history of hybridization may enjoy one or more potential genetic benefits relative to their progenitors. The observed lag times and multiple introductions that seem a prerequisite for certain species to evolve invasiveness may be a correlate of the time necessary for previously isolated populations to come into contact and for hybridization to occur. Hybridization may result in critical evolutionary changes that create an opportunity for increased invasiveness. Abbott (1992) observed that interspecific hybridization involving non-native plant species has often served as a stimulus for the evolution of entirely new, and sometimes invasive, species. Specifically, Abbott (1992) noted that hybridization involving a non-native species and another (either native or non-native) has led to a numeral new sexually reproducing plant species, which are either stabilized introgressants or allopolyploids. Some of these species have remained localized, but most have spread successfully far beyond their sites of origin.

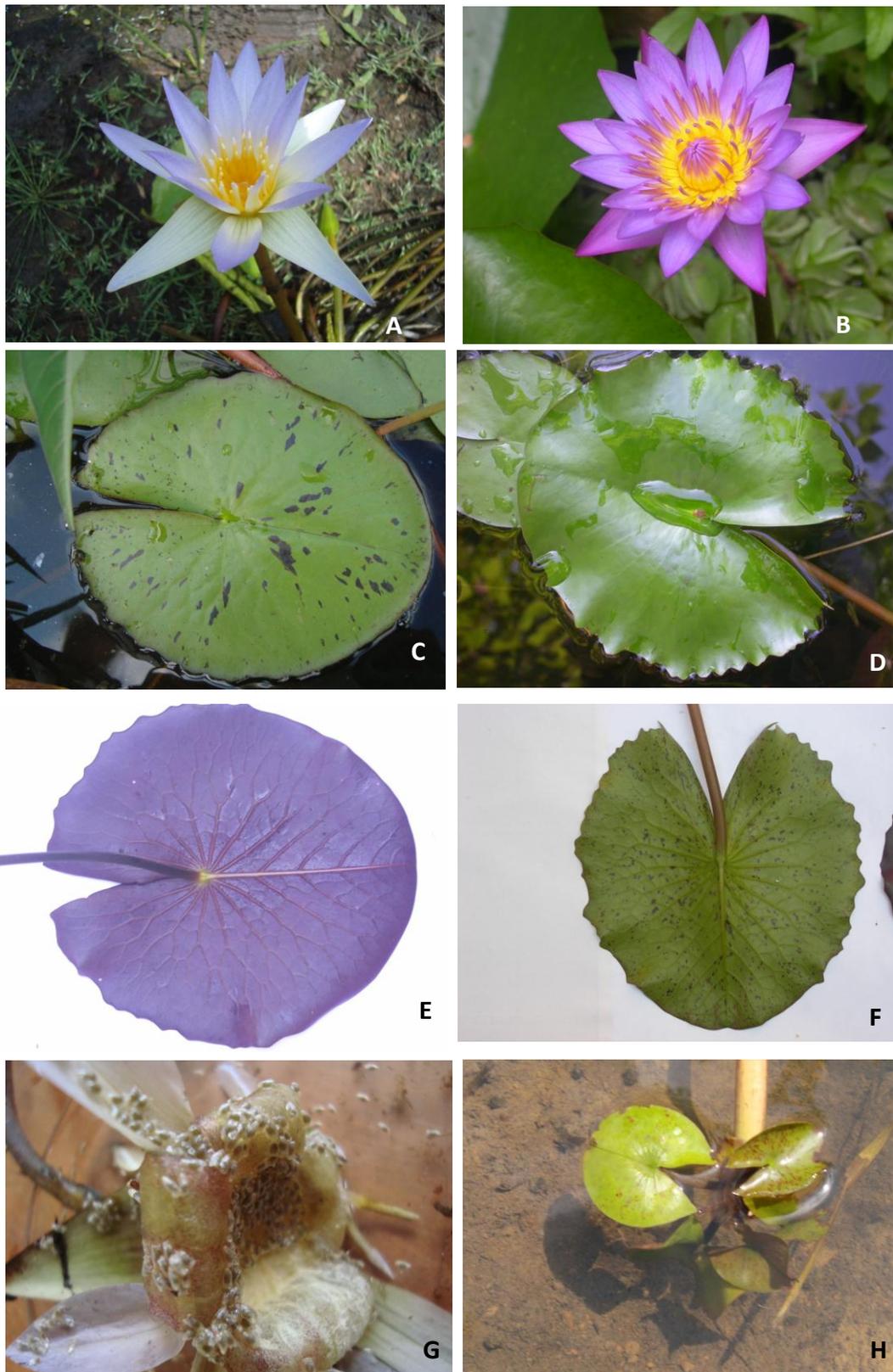
Tiebre *et al.* (2007) studying the pattern of hybridization and its evolutionary consequences of the invasive alien knotweeds, *Fallopia* spp. in Belgium observed a high level of genotypic diversity in the hybrid taxa compared to the parental species confirming the occurrence of interspecific hybridization among the *Fallopia* taxa in Belgium and the restoration of sexual reproduction by hybridization with the invasive alien *Fallopia* complex. This high genotypic diversity may increase the potential of the taxa to adapt and differentiate into new environments and contribute to the dramatic invasive success of knotweeds in their adventive range. In the absence of hybridization the interaction between the native and introduced species is essentially a competitive one between species that are similar in many aspects of their ecology and life histories. Assuming a homogeneous environment, without interbreeding, the species with the greater fitness (e.g. better competitor or higher reproductive rate) will dominate at equilibrium (Huxel, 1999).

Sri Lanka has experienced several breakthroughs of invasive alien species time to time. Even though Sri Lanka is blessed with a rich biodiversity, majority of plants used in agriculture, forestry, and ornamental plant industry are not native to the country. However, most of the plants that have been introduced are not invasive; they carry out their intended purpose and therefore benefit humans in multiple ways, causing no apparent problems.

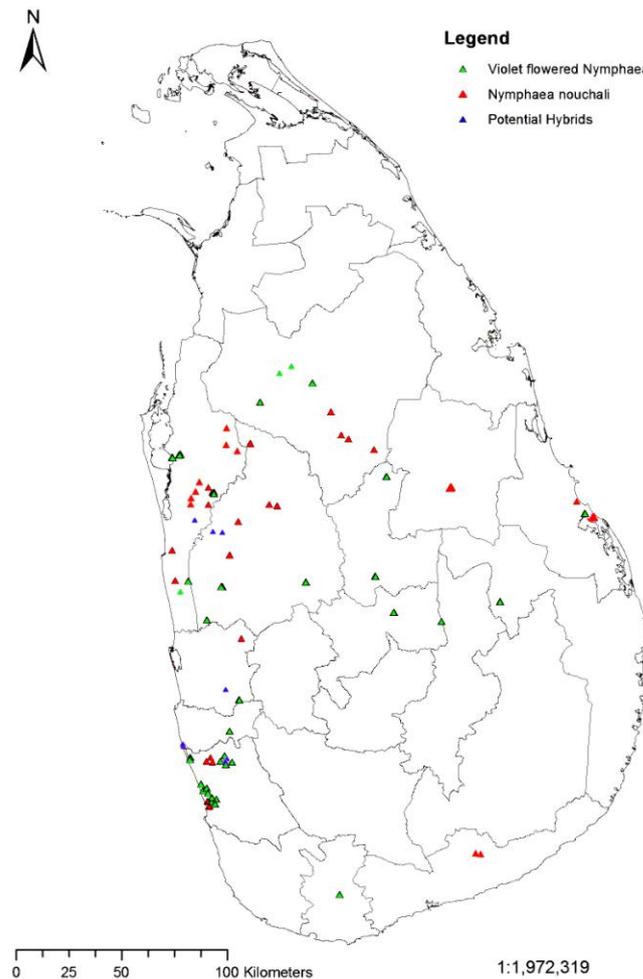
Nevertheless, a small proportion of the introduced plants that escaped from cultivation have become pests of natural areas. Many of such examples come from the ornamental plant industry where plants such as *Eichhornia crassipes* and *Lantana camara* have become serious invaders (Amarasinghe, 2001). While at present few other ornamental aquatic plants such as *Mayaca fluviatilis*, *Ludwigia sedoides* and *Echinodorus* spp. have been identified with the potential of invading the wet-zone aquatic ecosystems (Yakandawala and Yakandawala, 2007; Debarawatta and Yakandawala, 2009; Yakandawala and Dissanayake, 2010). Ornamental aquatic plant industry plays a leading role in the introduction of aliens into local water-bodies. Although Sri Lanka harbours a large number of naturally occurring aquatics, there is a demand for certain exotics in the export market and this has resulted in the importation of alien plants into the country, to be propagated and exported. According to statistics of the National Aquaculture Development Authority of Sri Lanka (NAQDA), 180 plants have been listed under ornamental aquatics and 87 are being propagated for exportation. Among them 123 have been identified as exotic species (Yakandawala and Yakandawala, 2007).

#### **A silent invader in local water-bodies: a case study**

Water-lilies have been popular as an ornamental aquatic plant in Sri Lanka from ancient times as they produce striking flowers throughout the year. They are represented in Sri Lanka by the genus *Nymphaea* L., and its two species, *N. nouchali* Burm. f. (Fig. 1, A, C, E and G) and *N. pubescens* Willd. (Dassanayake, 1996). In addition to these native water-lilies, few ornamental species have been introduced in the past where one species, a violet flowered *Nymphaea* (Fig. 1, B, D, F and H) has become naturalized. This plant has been incorrectly identified as *N. nouchali* by several authors (Kottegoda, 1994; Sumithraarachchi *et al.*, 1995; Samarakoon and Peiris, 2005; Mohan Maruga Raja, 2010). A preliminary investigation was initiated by the authors to identify and estimate the extent of the spread of this alien water-lily. Over 120 water-bodies covering all three major climatic zones of the island; Wet, Intermediate and Dry zones encompassing large, medium and small tanks, pools and ditches, were examined. The study revealed the abundant occurrence of the violet flowered *Nymphaea* species in 40% of the water-bodies (Fig. 2). The violet flowered



**Figure 1.** *Nymphaea nouchali* (A) Flower, (C) Leaf upper surface, (E) Leaf under surface, (G) Fruit with seeds. Violet flowered *Nymphaea* species (B) Flower, (D) Leaf upper surface, (F) Leaf under surface, (H) 15 -20 days old plantlets, still attached to the parent plant.



**Figure 2.** Map of Sri Lanka showing the collection sites of different *Nymphaea* species included in the study.

*Nymphaea* species has not only invaded the natural habitats of *N. nouchali*, but also has extended its territory into larger tanks inhabited by other aquatic macrophytes. The large floating leaves cut down a fair percentage of the light that penetrates into the water. Pure *N. nouchali* populations were encountered in 45% of the water-bodies (periphery of medium sized pools and ditches). The violet flowered *Nymphaea* is thought to have been introduced into the country as an ornamental aquatic long time ago, and has got established in local water-bodies. Studies on the nomenclature of the violet flowered *Nymphaea* is currently in progress (manuscript in preparation). Based on the studies conducted by the authors, the plant has been identified as a hybrid, with one parent being *N. micrantha* Gill.

& Perr. The other likely parent is either *N. capensis* Thunb., or *N. caerulea* Savigny. Its link to *N. micrantha* is due to the viviparous nature, as proliferating leaves are recorded only in *N. micrantha* that is native to Senegal, West Africa (Slocum, 1996; Wiersema, 1997). Crossing of the vivipary with other desirable factors is the ease in which these hybrids could be propagated, which is perpetuate through the young plantlets that grow upon the leaves of the parent plant.

Over thirty popular tropical day blooming viviparous cultivars have been developed with *N. micrantha* as a parent and are popular in aquatic landscapes (Knotts, 2003). *Nymphaea* ‘Tina’ and *Nymphaea* ‘Panama Pacific’ are two such cultivars that show features similar to the *Nymphaea* sp. with violet flowers found in Sri

Lanka. The latter is a viviparous variety that is said to be one of the hardiest of the tropics and also occurs in India (<http://botany.csdl.tamu.edu/FLORA/imaxxnym.htm>; and <http://www.flowersofindia.net/index.html>). The ability of this violet flowered *Nymphaea* to conquer the water-bodies of the island as a silent invader could be attributed to its hybrid nature. It is also possible that several introductions were also made into the country at different times, where the populations had the opportunity to mix and initiate the invasiveness, and the most suitable violet flowered hybrid getting established extending its territory. Meanwhile the ornamental value of it aided by the human involvement could have played a role in its spread. Due to the incorrect identification of the alien violet flowered *Nymphaea* species as *N. nouchali* ('Nil manel'), the national flower of Sri Lanka, at present this hybrid plays a prominent role in social, cultural and religious events. It does not produce viable seeds but reproduces by vivipary, which is an effective method of propagation and dispersal (Fig. 1, H). Virtually almost all the mature leaves are capable of producing a plantlet at the junction where the petiole meets the leaf lamina.

The present study also revealed populations of *Nymphaea* with intermediate characters (15%), indicating hybridization of the native *N. nouchali* with the alien violet flowered hybrid *Nymphaea* (Fig. 3, Hybrid I- A, C, E, G and Hybrid II- B, D, F, H and Table 1). The hybridization of invasive aliens with native flora is currently identified as a major threat that could lead to the extinction of the native flora (Levin *et al.*, 1996; Wolf *et al.*, 2001; D'Antonio and Meyerson, 2002). Wolf *et al.* (2001) investigated a number of ecological parameters likely to affect the extinction risk, through an individual based model that simulate the life cycle of two hybridizing annual plant species. It has revealed that, hybridization increased either the probability or the rapidity of extinction for one or both species studied. A study on two cordgrass species, a native and an invader, has revealed that due to the substantially higher male fitness of the invader, native cordgrass could be in danger of extinction (Anttila, 1998). Further, the same study revealed that the hybrids occupying the intertidal range are more similar to the invader than to the native parent, whose introgression would lead to habitat loss for shore birds and marine life as well to genetic pollution of native California cordgrass. Hybridization appears to contribute to species decline in two general ways (Ellstrand and Elam, 1993; Levin

*et al.*, 1996; Ellstrand *et al.*, 1999). If the hybrids display reduced fitness relative to either parental species (*i.e.*, outbreeding depression), the growth rate of the numerically inferior taxon may decline below that required for replacement (*i.e.*, demographic swamping). Alternatively, if hybrids are fertile and exhibit little or no decrease in fitness, they may displace pure conspecifics of one or both hybridizing taxa (*i.e.*, genetic assimilation). In addition, the decline of hybridizing species can often be attributed to the synergistic action of demographic swamping and genetic assimilation, and it may be difficult to distinguish between the two species (Wolf *et al.*, 2001).

Species that are most at risk to hybridization are out-crossing plants (Huxel, 1999). Further, displacement of native taxa by non-native taxa can occur very rapidly. Given the number of cryptic species and the high rates of human-mediated species introductions, extinctions may result from hybridization alone. Results have also indicated that introgression enhances displacement at low immigration rates, but impedes it when the native species has a large selective advantage and at higher rates of immigration. However, because of increased frequency of hybrids with introgression, the native is still heavily impacted and its likelihood of extinction is greatly increased. Nevertheless, it should also be noted that invasive alien species pose a hybridization threat proportional to their advantage over natives in the gene flow. Sympatry, interfertility, and rarity of natives are the characteristics previously seen to afford invaders a gene flow advantage (Ellstrand, 1992).

Island biota receives special attention in discussions as hybridization with IAS may be a significant threat to rare species on islands, thereby diluting the native gene pool to the point of extinction in a hybrid swarm (Reaser *et al.*, 2007). Examples of island plants threatened by hybridization with invasive plants include the common butterwort (*Pinguicula vulgaris*), which is locally rare in the British Isles, and Canary madrona (*Arbutus canariensis*) and Hawaiian ebony (*Gossypium tomentosum*), which are endemic to the Canary and Hawaiian Islands, respectively (Levin *et al.* 1996). There are no previous records on Sri Lankan invasives and, studies conducted in Sri Lanka have mainly focused on the impacts, control and management of IAS (Jayarathne and Ranwala, 2010). The present review is the first report on the interbreeding of a potentially invading plant species with a native species.



**Figure 3. Hybrids of *Nymphaea*; Hybrid I (A) Flower, (C) Leaf upper surface, (E) Leaf under surface, (G) Vivipary – note plantlets. Hybrid II (B) Flower; (D) Leaf upper surface, (F) Leaf lower surface, (H) Initiation of leaf vivipary.**

**Table 1. Comparison of morphological characters of parents and hybrids of *Nymphaea*.**

Morphological Character	<i>N. nouchali</i> (Native species)	Exotic violet flowered <i>Nymphaea</i> species	Hybrids of exotic violet flowered <i>Nymphaea</i> and native <i>N. nouchali</i>	
			Hybrid I	Hybrid II
Flower colour	pale blue/pink/white*	violet	violet	pale blue
Stamen number	12-50	> 120	>100	40-48
Stamen colour	faint yellow	bright yellow	bright yellow	bright yellow
Petal number	10-15	25-27	25-27	12-15
Leaf upper surface	green with occasional brown blotches	glossy dark green	green with occasional brown blotches	glossy green
Leaf lower surface	dark to light purplish green lower surface	light green with purple streaks	reddish purple with purple streaks	reddish purple with purple streaks
Vivipary	absent	present	present	present

\* Flower colour of *N. nouchali* varies from pale blue/pink/white. However, no sub-specific level taxa have been recognized.

#### Identification of invasives, a pre-requisite

Identification of these hybrid taxa from the parent taxa is important as eradication of such taxa in the early stage is an achievable goal (Castillo, 2010). Studies highlight the identification of the hybrid taxa as the base for studying the invasion ecology of congeneric species. Further, the basis for such a study lies in the identification of the parent taxa (Tiebre *et al.*, 2007). The present incorrect identification of the violet flowered *Nymphaea* species as native *N. nouchali* is a classic example where the former species is treated as a native as well as the national flower of Sri Lanka, overlooking the invasiveness. Similar example are hybrids of cordgrass, where genetically diverse, introgressive hybrids (Ayres *et al.*, 1999; Anttila *et al.*, 2000) between *Spartina foliosa* Trin. (native California cordgrass) and *S. alterniflora* Loisel (alien - Atlantic smooth cordgrass) originated in the tidal salt marshes of San Francisco Bay following the introduction of Atlantic smooth cordgrass, into the range of the native California cordgrass (Ayres *et al.*, 1999; Faber, 2000). Early workers (Callaway and Josselyn, 1992; Daehler and Strong, 1994) assumed that the cordgrass invader was Atlantic smooth cordgrass. Nevertheless, later work using molecular markers suggested that the plants invading new sites were hybrids and that pure Atlantic smooth cordgrass plants were common only in sites where they were initially planted (Ayres *et al.*, 1999; Ayres, *et al.*, 2008). Therefore, identification of newly formed hybrids using morphological characters alone

may lead to an underestimation of the true extent of species diversity (Petit, 2004; Lopez *et al.*, 2005; Mallet, 2005). Combining morphological and molecular data would be an efficient tool for differentiating taxa within complex populations (Persson and Gustavsson, 2001; Cattell and Karl, 2004).

Revealing the flawed identity of the *Nymphaea* with violet flowers, its hybrid origin and the hybridization with native *N. nouchali*, will open up new avenues in research in invasions of aliens to Sri Lanka. These findings provide an excellent opportunity for initiating studies locally on this novel area of hybridization between natives and invasive alien species. Further, this could be extended to analyze the genetic and evolutionary consequences of hybridization, an overlooked threat to the biodiversity of Sri Lanka.

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